Journal of Research on the Lepidoptera 12(3):151-160, 1973

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SURVEY OF ULTRAVIOLET REFLECTANCE OF NEARCTIC BUTTERFLIES

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THERE HAS BEEN INCREASING interest in the role of ultraviolet in insect-insect and insect-plant interactions. In particular, it has been found that in some butterflies, males use the ultraviolet reflectance of females in intraspecific sexual communication (Obara, 1970). The purpose of this paper is to survey the ultraviolet reflectance of a wide variety of North American butterflies and skippers. This survey will enable future workers to effectively select taxa for detailed experimental studies of the functional utility of ultraviolet reflection. Previous research has been mostly on Pieridae and a few large tropical species of other families, but this study shows that many taxa have "hidden" ultraviolet reflectance patterns just as spectacular and deserving of study. Generalizations about ultraviolet-reflection are made which contribute to knowledge of the relative roles of male and female in the mate-locating process, and of the utility of ultraviolet as an isolating mechanism. This study suggests that a wide variety of behavioral responses to ultraviolet must occur in various taxa because of the great diversity of ultraviolet-reflectance systems.

METHODS

14,000 Papilionoidea and Hesperioidea of about 1000 species from the United States, Canada, and northern Mexico including all species endemic north of Mexico were photographed in full natural noon October sunlight using a Tiffen 18A filter (maximum transmission 360 mu, 0.1% transmission at 305 and 400 mu) using a 4 by 5″ Speed Graphic camera with a 127-mm Kodak Ektar lens and Polaroid type 52 black and white film (ASA 400), at F11 and 1/50 sec. U-V reflectance was not quantified for the purposes of this survey. Natural variation of ultraviolet is very great (for instance, ultraviolet intensity varies throughout the day, full noon sunlight has twice the intensity of ultraviolet in

June-July as in April and October, and clouds absorb most ultraviolet) so that quantification was not thought to be critical for this brief survey. For detailed studies, spectrophotometry especially, or the techniques of Robert Silberglied (1973, PhD thesis, Harvard University), should be used. The lens and filter used enables ultraviolet only in the approximate range of 350-400 mu to be recorded on film; therefore some reflectance patterns from 300-350 mu may have been missed, although the range 300-350 mu is a minor component of natural ultraviolet, and previous work on one species (Obara, 1970)showed that only the range 380-400 mu was behaviorally used. A four-letter system was used to describe relative ultraviolet reflectivity: a—weakly reflective, appearing dark in photos; b—moderately reflective, appearing gray in photos; c—quite reflective, appearing light in photos; s—structurally reflective, appearing white in photos (structural reflection did not always appear white). This rough system approximates actual reflectivity, and for detailed studies spectrophotometry is advised. D—dorsal, V—ventral, FW—forewing, HW—hindwing.

RESULTS

A. *Papilionidae* 1) In *Parnassius,* white and yellow mostly absorb ultraviolet, females reflect more than males, and V reflects similar to D. *P. phoebus* is slightly more reflective than *P. clodius.* 2) In *Battus philenor* the white spots of some males and of most females reflect strongly on the HW but rarely on FW; the bluish sheen reflects slightly. In *B. polydamas* the lighter yellowish bands do not reflect. 3) In *Graphium marcellus, G. epidaus,* and *G. philolaus,* V reflects more (c) than D (b) light areas. Greenish ground color reflects very slightly, but in *G. epidaus* the wings are uv-transparent. In *G. phaon,* the blue or red spots either absorb, or reflect slightly. 4) In the *Papilio glaucus*-group, V reflects slightly more than D. Postmedian D and V blue spots reflect (s). In *P. glaucus* and *rutulus,* males absorb D, females absorb D or reflect slightly, and both sexes reflect slightly V (b, rarely c).In *P. multicaudata* both sexes absorb D, reflect slightly V. In *P. eurymedon* both sexes reflect D (b), slightly more V. 5) *P. troilus*-group and *P. victorinus.* In some female *troilus,* some female *palamedes,* and some male and female *pilumnus,* the postmedian blue spots are present and reflect (s). VHW median white crescents reflect in at least *troilus* and *pilumnus.* The greenish (in *troilus* and *victorinus*) and yellowish spots absorb except occasionally reflect slightly in *pilumnus.* 6) In the *Papilio machaon*-group blue postmedian spots reflect (s). V is more reflective (c) than D. VHW median crescents sometimes reflect as in *P. troilus.* Black forms absorb dorsally. Yellow forms mostly absorb D, with a few males and some females more reflective (a to c). In *P. polyxenes "clarki", bairdii "hollandi"*, and a few *P. p. polyxenes,* the D yellow bands of dark forms sometimes reflect (b). In *P. indra,* D bands reflect slightly in ssp. *indra, minori* and most *pergamus,* and reflect moderately in ssp. *martini, fordi,* and some *pergamus.* 7) In the *Papilio cresphontes* group, V reflect slightly more than D. Postmedian blue spots reflect (s). D yellow bands usually absorb, occasionally reflect (b) especially in females. 8) In *Papilio garamas,* the yellow absorbs dorsally and reflects slightly on the postmedian band VFW (b), but the apical VFW and VHW yellow are highly reflective (c). 9) In *Parides arcas,* the male green spots absorb, and the female white spots reflect only slightly. In *P. arcas* and *P. anchisiades,* the red spots reflect somewhat.

B. *Pieridae* (*Euchloe*). My results on Pieridae other than *Euchloe* are not presented because Robert Silberglied is preparing an extensive worldwide survey. 600 individuals of *Euchloe ausonides* were photographed, in connection with prior (Scott 1973) behavioral studies. Small numbers of *Euchloe hyantis* and *E. creusa* were photographed for comparison.

Ultraviolet reflectance of *E. ausonides* was found to vary between D and V, between sexes, between seasons, between individuals, and between localities. 1) *Upperside.* Males are non-reflective; females are almost always slightly reflective. Some females are very reflective, appearing white in the photos. The very yellow dorsal areas on females are usually ultraviolet absorbing; the dorsal hindwings of females are usually yellow and are often more absorbing than DFW. There is poor correlation between the yellow color and uv-absorption, as some very yellow females are very reflective and some white females are relatively non-reflective. 2) *Underside.* The forewing reflects similarly to the D of females. Females have approximately the same reflectivity as males, except that the lightest (most reflective) individuals are females. The female D variation does not occur on V. The green and black ventral spots absorb ultraviolet.

3) *Geographic variation.* California populations (*E. ausonides ausonides*) are variable on the female upperside, but Colorado populations (*E. ausonides coloradensis*) are almost invariant. 32 of 61 females from Point Richmond, Contra Costa County, California, but only 4 of 71 females from throughout Colorado, were highly reflective (white in ultraviolet photos). In all the Colorado individuals the white on VHW was very reflective, but in 11 of 70 males and 18 of 61 females from Point Richmond this white area absorbed ultraviolet and photographed almost as darkly as the green spots. Few individuals of *E. ausonides ausonides* from other areas were photographed, but variation similar to that in California may occur because females from Montana and the Yukon were reflective above, and two females from northwestern Wyoming and Utah absorbed ultraviolet on VHW.

4) *Seasonal variation.* The female dorsal polymorphism is not seasonal, as very reflective females occurred throughout the California flight period from March 3 to June 14. Non-reflective VHW individuals, however, at Point Richmond occurred only after May 16 except for one male caught on April 26 and two intermediate individuals taken in April. *Euchloe* has only one brood, except in central coastal California, where May 16 is the onset of the second mode of emergence (Opler, 1968), and very rarely has a second mode in early July in the Colorado foothills. The second brood apparently represents late emerged individuals, because I found that Point Richmond pupae have obligatory diapause.

5) Several other Euchloe species were photographed; they reflect differently than *E. ausonides*. *E. hyantis* shows little variation on the upperside; both sexes are equally reflective and resemble female *E. ausonides* from Colorado (males are more reflective than *E. ausonides* males). *E. hyantis* from Lake Tahoe, California, often have VHW with white areas which absorb ultraviolet. *E. creusa* males are reflective like *E. hyantis* males but females are variable in reflectance, as in *E. ausonides*.

C. *Libytheidae.* The fulvous color mostly absorbs; white spots reflect.

D. *Nymphalidae.* The red of *Anaea andria* and *A. aidea* absorbs, but in *A. glycerium* red males reflect moderately while red females reflect slightly. In *A. pithyusa* the blue reflects only slightly. The yellowish of *A. echemus* reflects (b). In *Apatura* and *Limenitis* (includes *Adelpha*), orange spots completely absorv uv. The DFW of *A. laure* appears mostly black in the photos with a reflecting spot at the anal angle continuing as the DHW reflecting white stripe, whereas in *A. pavon* the wings strongly reflect (s) over most of D, which is purplish black. In female *Apatura,* only the white stripe reflects (c). The V of *A. laure* has a silvery sheen which reflects more than V of *A. pavon.* The white bands of *Limenitis* spp. (and several *Adelpha* spp.) reflect strongly except that those of *L. lorquini* and *L. bredowii* are slightly yellowish and reflect only slightly. The V red of *L. arthemis* absorbs. *L. arthemis astyanax* appears identical in uv and normal photos. *L. archippus* and *Danaus* spp. absorb uv and appear very similar, although Texas (but not Florida) *D. gilippus* reflects slightly more and the wing veins of Texas *D. gilippus* usually reflect uv. In individuals of both sexes of *Myscelia,* and in male *Eunica,* all the wings reflect (s) except the border which is wide in *M. cyananthe.* In uv photos *Biblis* and *Hamadryas* appear identical to visual appearance except *H. ferox* is more reflective dorsally. The red of *Biblis hyperia* reflects structurally, and reflects strongly V. The white of *Mestra* reflects strongly. The red of *Hypanartia* and *Marpesia petreus,* the D brown of *M. chiron,* and the metallic green of male *Dynamine* absorb uv. The V of *Marpesia* reflects (b), and the white V bases of *M. chiron* are highly reflective. The bluish sheen of *Bolboneura sylphis* reflects, (s). The red and fulvous of *Asterocampa, Vanessa,* and *Nymphalis* absorbs, and white spots reflect. The FW and HW apical white spots of *N. vau-album* reflect strongly, but the FW apical white spots of other *Nymphalis* are less reflective. The marginal blue spots of *N. antiopa* are highly reflective (s), but the yellow border absorbs. The orange bands of some *N. milberti* reflect slightly basally. In *Precis,* only the anterior DHW eyespot (c), and DFW apical band (a-b) reflect and only in individuals in which these areas are not darkened. The white of *Anartia* reflects (only moderately in some *A. fatima* with slightly yellowish bands) and the fulvous and red absorbs. *Metamorpha* appears similar in uv and normal photos. The fulvous of *Polygonia,* Melitaeini, and Argynnini absorbs, and white spots reflect except that cream-tinged whitish areas (as in *Morpheis ehrenbergi* D and *Chlosyne palla* VHW) reflect only moderately. The lighter fulvous bands of some *Chlosyne theona* and *C. leanira* (some *fulvia,* but no *leanira, alma,* or *cyneas*), some *C. palla* females, and some *C. acastus* (especially a light population from Snake River, Baker County, Oregon) reflect moderately. *Euphydryas phaeton* almost uniformly absorbs, but in other *Euphydryas* in some individuals and populations the light spots reflect somewhat. The silvery V spots of *Boloria, Speyeria,* and *Agraulis* reflect (s). The light color of female *Speyeria nokomis* and some female *S. cybele* reflect slightly. The blue or metallic color of *S. diana* females and *S. idalia* does not reflect greatly. In Heliconiini, yellow, orange-fulvous and red areas mostly absorb dorsally, but usually reflect ventrally (slightly in *Colaenis* and *Heliconius isabellae;* (b-c) in *H. charitonius* and *H. erato*). In *Morpho* species, blue structurally reflects ultraviolet but not as strongly as the white of the white species. In Satyrinae, brown, red, and fulvous areas usually absorb ultraviolet. White V markings reflect. Some whitish *Coenonympha tullia californica* individuals reflect moderately. The white of *Euptychia hesione* reflects strongly. *Lethe* females have some slightly reflective lighter areas. The yellow patches of *Cercyonis pegala* sometimes reflect slightly. The white spots of *Gyrocheilus* D reflect.

E. Lycaenidae. 1) Riodininae. White spots reflect. The orange-brown areas of *Apodemia*, *Calephelis, Caria,* and *Emesis* absorb uv, as do the yellow and red spots of *Lymnas, Baeotis hisbon, Argyrogramma sulphurea,* and *Euselasia eubule.* The blue of *Lasaia* and *Anteros carausius* reflects only slightly, but the blue of *Theope virgilius* and *Mesosemia telegone* reflects strongly (s) (including FW postmedian, median, and basal area of *M. telegone*). In *Anteros carausius* the hyaline spots reflect dorsally and ventrally, and the yellowish V basal bar reflects strongly.

2) Theclini. Blue areas are very reflective (s), despite the visual shade (from dark metallic blue of *Ocaria ocrisia* to slightly violet-tinged white of *Thecla meton* males and the violet of *Hypaurotis crysalus*); the following exceptions were noted, which have only weak reflectance: *Panthiades m-album, Atlides halesus,* male *Thecla regalis* (in these three species the female reflects more than the male), males of *Thecla phoenissa, T. janais, T. lyde, T. carla, T. schausi, T. hemon,* and *T. mavors* (D and V, which are metallic green in *mavors*). Reddish brown, brown, and red absorb. Green generally absorbs. White areas of *Thecla meton* females reflect (c). V of many tropical Theclini is highly reflective, and V of most other species is usually more reflective than D. The D green of *Eumaeus deborah* mostly absorbs, the V spots reflect, while the marginal DHW spots (and a blue DFW cell streak of a female)

of *E. atala* reflect fairly strongly. *E. minyas* is intermediate.

3) Lycaenini. Males of some species reflect D, but females are non-reflective. V often lighter than D (usually slightly more, but (c) in *xanthoides* and *heteronea*). The anal angle is non-reflective on male DHW; the non-reflective margin is very narrow in *Lycaena heteronea,* narrow in *L. gorgon,* broader in *L. mariposa* and *L. rubidus,* and broadest in *L. arota.* The following descriptions refer to males unless otherwise indicated. *L. phlaeas* reflects weakly in both sexes. *L. cupreus* (includes *snowi*) males and females reflect more strongly. In *L. mariposa, L. gorgon, L. rubidus,* and *L. heteronea,* males reflect (s) except for a narrow border and the DHW anal angle. In *L. gorgon,* the whitish DFW spots of one female reflect somewhat. In *L. nivalis, L. helloides, L. dorcas, L. epixanthe,* and *L. thoe,* males reflect (s) except for a narrow border DFW and a broad border DHW, which are non-reflective. In *nivalis,* the D. border is narrower than in the other four species. In *helloides,* whitish females from Yellowstone National Park and southern Montana reflect moderately. In *L. thoe,* the DFW border is narrower, and DFW orange of some females reflects slightly. *L. xanthoides* and *L. editha* are non-reflective. In one *xanthoides* female, submarginal D blue spots reflect. *L. hermes* is non-reflective. *L. pyrrhias,* and *L. arota* reflect all over D wings (s) except a narrow border and the anal DHW angle.

4) Plebejini. Orange mostly absorbs. The blue of males (and females when present) structurally reflects strongly (s). The white of some *Leptotes* and *Celastrina* females reflects strongly. V is usually more reflective than D, and reflects strongly when nearly white as in *Everes* and *Celestrina.* Greenish-metallic color reflects ultraviolet much less (slightly in *Lysandra coridon* from Europe and in *Agriades;* moderately in *Plebejus saepiolus* and in some *P. shasta* populations especially near timberline in Colorado, where some colonies are greenish (moderately reflective) and others are blue (c); (b) in the greenish *P. lupini chlorina,* usually moderately, sometimes strongly reflective in the blue *P. lupini lupini* and *P. l. monticola* (c in *P. acmon*)).

F. Hesperiidae. Fulvous and yellowish colors mostly absorb ultraviolet, with slight differences between species and individuals. White and hyaline spots usually reflect, with some exceptions noted below. In *Megathymus streckeri* and *M. beulahae,* some *M. yuccae* and *Agathymus mariae,* postmedian fulvous bands reflect slightly. *Atrytone arogos* is slightly more reflective than other Hesperiinae species including *A. delaware*. The white of *Heliopetes* absorbs or reflects ultraviolet (a to c); *H. ericetorum* is especially variable. The pure white areas of *Atarnes sallei* absorb, and the white areas of *Onenses hyalophora* and *Polyctor polyctor* refflect only moderately. In contrast, the white areas of *Theagenes albiplaga, Chiomara,* and *Mylon lassia* reflect strongly. The white spots of *Pyrgus* and *Xenophanes* absorb, or reflect strongly. The white hyaline spots of *Zestusa dorus* usually absorb but sometimes reflect moderately. The yellowish hyaline spots of *Achalarus lyciades* absorb, while those of *Autochton cellus* reflect slightly. The bluish colors of some *Astraptes*, *Aguna*, *Epargyreus*, and *Urbanus* reflect uv only weakly.

DISCUSSION AND CONCLUSIONS

The following taxa other than Pieridae seem to hold the most promise for experimental studies of the behavioral use of ultraviolet reflectance: *Papilio eurymedon* and relatives, many tropical Nymphalinae, Charaxinae and Morphinae, many tropical Riodininae and Theclini, most Plebejini and *Lycaena,* and some Pyrginae (especially some tropical species).

Tropical species have a greater variety of ultraviolet reflectance patterns than do temperate species, and are more often ultraviolet-reflective.

White and blue, or a metallic sheen over other colors, are usually uv-reflective, and black, brown, fulvous and green usually absorb ultraviolet. The color cannot be used to predict uv-reflectance, however, because of many exceptions; white, yellow, orange, and brown-black, etc., may absorb or greatly reflect ultraviolet in various taxa, and the same color on the same wing may reflect differently dorsally and ventrally (*Papilio garamas, Neophasia terlooti,* etc.). Since there are two means of producing ultraviolet reflection, pigments and structural interference (Ghiradella et al. 1972), this is not surprising.

Males are much more likely to have highly reflective areas than are females. This fact, together with the more common presence of presumed pheromone-producing structures in males, underscores the usual role of the male in making a female receptive for mating, while the female's role is usually in passively deciding whether to allow the male to copulate. Ultraviolet reflection is often similar in closely related species (for instance, *Lycaena rubidus, L. heteronea,* and *L. arota* are dissimilar in color (red, blue, and brown on D of males) but all males are highly uv-reflective). In these taxa the ultraviolet reflectance may be used by the butterfly to distinguish between the sexes, and other stimuli such as pheromones and non-ultraviolet color may be necessary to distinguish between species.

The ground color of females is often slightly more reflective than ground color of males, especially in Pieridae; great sexual dimorphism, as in *P. rapae crucivora* (but not *P. rapae rapae*) may enable males to distinguish between the sexes (Obara, 1970).

The great variety of systems of reflection of male versus female and D versus V casts doubt on a single behavioral explanation of the use of ultraviolet reflection during mating behavior. In Pieridae especially, the behavioral findings of Obara (1970) may not apply to many species (or even to *P. rapae rapae*). In *Neophasia terlooti*, for instance, in which males are white and females red, J. W. MacSwain (oral communication) caught numerous males which came to red plastic cups; the similarity of ultraviolet reflectance of both sexes may mean that the red color rather than an ultraviolet cue is sought by males. In other species, individual variation in reflectivity complicates the situation (*Papilio machaon*-group, *Euchloe*, *Kricogonia*, Heliopetes, etc.). In some cases, ultraviolet reflection might be used to distinguish between the sexes but not between species (*Phoebis philea* and *Anteos chlorinde* have nearly identical ultraviolet reflectance patterns, as do *Eurema lisa* and *E. nise*, etc.). In other cases, the species may be distinguished using ultraviolet only in one sex, usually the male (some *Eurema*, etc.).

V is usually more reflective than D. D may be darker to absorb more solar energy (mainly non-ultraviolet) during basking, which is usually done by spreading the wings, and ultraviolet absorption is usually correlated with darker color. In some taxa which bask by closing the wings and positioning VHW perpendicular to the sun's rays, such as some Pieridae and Theclini, there is little difference in D and V reflectivity. In *Pieris rapae crucivora*, the difference between D and V in reflectivity may be used to maintain the reflectivity (Obara, 1970); in cool or cloudy weather individuals bask by spreading the wings exposing the more reflective D, and because more ultraviolet is absorbed by the atmosphere when cloudy or when solar radiation passes obliquely through the atmosphere in early morning and late afternoon when cool temperatures are frequent, the same D reflectivity may be produced as from V at midday or in warm sunny periods.

In some species there is variation of uv-reflectance in which spring individuals are more reflective (*Euchloe ausonides*, *Plebejus acmon* female D). This variation may also make ultraviolet reflectance more similar in spring and summer, because the sun's rays pass through the atmosphere more obliquely in early spring than in summer.

Structurally produced ultraviolet reflection differs from reflection produced by pigments in that the wings may reflect only when viewed at certain angles, which would produce intermittent flashing of ultraviolet by a flying individual. This may serve as an isolating mechanism if the flashing in addition to the static reflectance pattern is utilized by mate-seeking individuals (Crane, 1954).

ACKNOWLEDGMENTS

I thank Dr. Richard B. Taylor, U. S. Geological Survey, Denver, Colorado, who greatly assisted with the photographic apparatus, and Robert Silberglied, Harvard University, who criticized a previous manuscript.

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